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The relation of chromosome pairing to fertilization

G. M. Watkins

During the decades which have elapsed since the modern cytological studies by Strasburger, van Beneden, Boveri, and others on sexuality in plants and animals the concepts as to what constitutes fertilization have changed markedly. Still earlier, as summarized by Johnson (1914), conjugation in *Spirogyra* was observed by Hedwig in 1798 and by Vaucher in 1803, in the Zygomycete, *Syzygites* (*Sporodinia*), by Ehrenberg in 1818, and in several species of desmids (*Closterium*) by Ehrenberg (1838). Unger in 1834 described the spermatozoids of *Sphagnum*, while Thuret (1854) for *Fucus* and Pringsheim (1855) for *Oedogonium* gave perhaps the first accounts of the fusion of heterogametes in the algae. The union of unlike gametes was also discovered in the Oömycetes about this time. Tulasne in 1854 observed the sexual process in *Peronospora*, and de Bary (1863) observed and figured the flow of gonoplasm from the antheridium to the egg in *Pythium*, and also figured a similar process for *Cystopus*. This was perhaps the first and is probably still the most convincing account of a genuine mixing of plasms in a case in which the sex differences characterizing maleness and femaleness are well marked. Fertilization by mixing through a fertilization-tube was seen in *Saprolegnia* and *Achlya* by Pringsheim (1858). Spermatozoa were seen within the ova of the rabbit by Barry (1843).

In spite of de Bary's development of the gonoplasm concept, the majority of early workers came to regard fertilization, especially in algae and fungi, and on the basis of the *Spirogyra* data, as the "fusion of two apparently homologous cells." This view involved primarily the union of protoplasts, without particular regard to the activities or fate of the various cell constituents.

This concept of fertilization dominated biological thought until the studies of Hertwig (1877 a and b), Strasburger (1877), and Schmitz (1879) revealed that in both plants and animals the union of the gametic protoplasts may be followed directly by the fusion of gametic nuclei. The most advanced view, perhaps, of that time was expressed by Strasburger (1877, p. 509) in the following generalization:

"O. Hertwig ist der Ansicht, dass die Befruchtung allgemein auf der Copulation zweier Kerne, des Kerns des Spermatozoiden und des Eikerns, beruht, in dieser Ansicht stimme ich mit ihm überein, erweitere sie aber darin, *dass*

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eine Copulation auch zwischen den übrigen gleichwerthigen Bestandtheilen des Spermatozoiden und des Eies vor sich geht."[1]

In this contribution Strasburger definitely committed himself to the view that fertilization consists of more than a gross plasmatic fusion. It involves also a union of equivalent parts of the gametes. Schmitz (1879) upheld this view by showing in stained preparations that gametic nuclei of *Spirogyra* move together and fuse after the protoplasts have united. That the behavior of the nuclei in the zygospore of *Spirogyra* is as simple as Schmitz reported was later brought into doubt by the work of Chmielevsky (1890).

Further evidence that protoplasmic fusion (plasmogamy) is followed immediately by the union of gametic nuclei (karyogamy) appeared in the expansive and careful studies by van Beneden (1883), Boveri (1890), and many other workers. This came to be regarded as the essential characteristic of fertilization, and subsequent data have shown that syngamy of this type occurs in the majority of plants and animals. During this period, however, Klebahn (1888) showed that in many Conjugatae plasmogamy occurs without being immediately followed by karyogamy. A thick-walled binucleate zygote is produced, which may endure thus, as he reports, for many months, finally undergoing karyogamy at the time of germination. Raciborski (1896), in studying zygote formation in *Basidiobolus ranarum*, by controlling the cultural conditions was able to delay karyogamy for varying lengths of time. In some cases the binucleate zygote was caused to germinate, producing, as reported, a binucleate germ-tube. Raciborski concludes that two definite phases are to be distinguished in fertilization, namely, fusion of protoplasts as wholes and fusion of gametic nuclei. In case plasmogamy is separated from karyogamy by a dikaryophase of several or many cell generations, the cell in which the nuclei at last fuse was termed by Raciborski the *zeugite*. In animals a similarly delayed karyogamy was described for *Cyclops* by Rückert (1895) and Häcker (1895), who showed that the individuality of the parental nuclei is maintained through several successive gonomeric divisions in the early development of the embryo. Later B. G. Smith (1919) demonstrated a similar condition in *Cryptobranchus* extending in all nuclei of the embryo through the fourth cleavage mitoses.

Poirault and Raciborski (1895) and Sapin-Trouffy (1896) found that karyogamy takes place in the Uredinales in the mature teleutospore, thus ending the long dikaryophase which had been known (Schmitz, 1880) to exist throughout most of the rust life cycle. It was later shown by Blackman (1904), Christman (1905, 1907), and Blackman and Fraser (1906)

[1] My italics.

that the dikaryophase in several species is initiated by nuclear migrations or cellular fusions in certain sub-aecidial hyphae. Thus far the data on sexuality in fungi and algae left unsettled the question of the function of the spermatia in the rusts. According to Meyen's (1841) early suggestion, the products of the spermogonia and aecidia are to be regarded as male and female gametes respectively, and Blackman's figures of nuclear migrations tend to uphold this, indicating, however, that the spermatia are vestigial male gametes and that certain vegetative hyphae near the "female" hyphae in the base of the aecidium have become transformed into functional male gametangia. The studies of Craigie (1927 a and b, 1928, 1931), pointing out the heterothallic nature of some rusts, and that the union of the products of plus and minus strains of sporidia is necessary for the production of aecidia, marked the beginning of a new epoch in the study of sexuality in fungi. Miss R. F. Allen (1930, 1932, 1933) and Andrus (1931) report that the binucleate condition may arise perhaps by the fusion of spermatia with certain receptive hyphae which protrude through the stomata of the host. Andrus has compared these receptive hyphae with the trichogynes of the red algae and many ascomycetous forms. As suggested by Miss Allen (1933, p. 11), the recent discovery of fertilization through the union of spermatia with receptive hyphae seems incompatible with the older accounts of Blackman and Christman. Considered from the present-day standpoint it seems that different species of rusts may differ in the manner of origin of the binucleate condition, yet it is nonetheless characteristic of the majority of species so far investigated that the entire sporophytic phase is composed of binucleate cells, karyogamy in the mature teleutospore being followed immediately by meiosis and a return to the haploid condition.

The rise of interest in heredity during the last thirty-five years has directed much attention to nuclear phenomena, and especially to the chromosomes, since evidence points to them as the possible conveyors of hereditary and morphogenetic factors. In this connection one of the most important characteristics of the nuclear constituents is the so-called paired condition of the diploid chromosomes, which supposedly is the attainment of the definitive relations between the parental chromatin elements. If indeed the chromosomes are the primary carriers of hereditary factors, it is in this relation only, according to current views, that these factors can be blended, balanced, and distributed to the posterity of the organism. Thus fertilization has come to be considered as essentially the conjugation of homologous chromosomes, which, in the possibilities thus achieved, provides for crossing over, translocation, segmental interchange, etc. In the above quotation from Strasburger may be seen an early forecast of this

idea, and another interesting view was expressed by Johnson (1914):

"The essence of the sexual process then, as far as yet morphologically demonstrated, consists not of a real fusion, but merely of a temporary association, followed by a reassortment at sporogenesis, of those ultimate, inheritance-bearing units—the chromosomes."

In the majority of plants and animals studied the chromosomes are so far figured and described as paired only in meiosis, at the end of the diploid phase of the life cycle. But evidence by Strasburger (1905), Müller (1909, 1912), Metz (1914, 1916), and many others shows that in certain species of plants and animals the chromosomes are paired during divisions of diploid somatic nuclei. Among plants *Yucca aloifolia*, *Y. draconis*, *Y. guatemalensis*, *Galtonia candicans*, *Pisum sativum*, *Oryza sativa*, and others, and among animals a large number of species of the Diptera exhibit paired chromosomes in somatic mitoses. This pairing, as figured in the literature, is usually not as close as that found later at synapsis, as can readily be determined by comparing the mitotic figures given for such forms by Strasburger (1905, 1907), Müller (1909, 1912), and Metz (1914, 1916) with, for example, those of C. E. Allen (1905) for the synaptic and post-synaptic stages of *Lilium canadense*. It, however, indicates an expression of the same tendency, the earliest possible expression of which is the pairing of the chromosomes immediately during and after karyogamy.

Recent reports by Heitz and Bauer (1933) and Painter (1934) indicate that such complete chromosome conjugation may not necessarily be confined to the meiotic prophases. In follicular cells of the ovary, cells of the malpighian vessels, salivary glands, and intestinal walls of *Bibio hortulanus*, Heitz and Bauer describe prophase figures in which bivalent chromosomes corresponding to the haploid number are seen. According to their figures the members of each pair can be seen to conjugate point for point throughout the entire length of the homologues, until complete synapsis is accomplished. These figures (Heitz and Bauer, 1933, figs. 1a and 2a-c) are strikingly similar to the late prophases of meiosis, particularly diakinesis, with the homologous chromosomes closely paired and showing numerous chiasma-like unions. As figured by them the prophases of mitosis in these cells are essentially like typical meiotic prophases, with the exception that the synizesis or contraction stages are lacking. Painter's account of the conditions in the salivary glands of *Drosophila melanogaster* agrees essentially with the report of Heitz and Bauer, with the additional observation of the failure of pairing in certain segments of the bivalents where inversions were said to have occurred. It is highly interesting and significant to

note this departure from the older concepts of synapsis as an event peculiar to meiosis. According to the current views of crossing over, segmental interchange, etc, and the genetical data based on them, the homologous chromosomes have been regarded as bodies remaining discrete and immiscible throughout the thousands of successive somatic mitoses following fertilization, but changing character more or less completely during the brief period of meiosis involving intimate conjugation, sticking together, and interchange of parts. These views, postulating a high degree of particulate specificity in the relation of the conjugating chromosomes, are hardly compatible with the present-day conceptions of the colloidal nature of protoplasm. If the union of homologous chromosomes in somatic cells is as intimate as that described by Heitz and Bauer and by Painter, there is no *a priori* reason why chiasmatypy should not characterize somatic as well as meiotic synapsis. In general the widespread occurrence of non-meiotic synapsis and crossing over, especially in cells destined to give rise ultimately to the reproductive cells, would provide the mechanism for almost any assumed heterogeneous or alternative types of inheritance as well as the mendelian, and would perhaps afford a better basis for the assumption that the chromosomes are the material of heredity. However, the manifestation of mendelian inheritance by an organism in which somatic synapsis is a general occurrence might be taken as implying that the characters of the progeny are determined by some extrachromosomal agency. The implication is very strong that the promiscuous occurrence of synapsis in somatic nuclei, with the attendant manifold possibilities of chiasmatypy, is incompatible with the assumption of the genetic individuality of chromosomes with the genes in a linear series.

Miss Fraser (1912) has pointed out the wide variations in the behavior of parental chromatin elements following syngamy in different organisms, emphasizing especially the marked differences between such forms as *Galtonia candicans*, in which the chromosomes are paired in somatic divisions, and the rusts, in which karyogamy does not occur until almost the end of the diploid phase. Abundant data in this connection have been accumulated since the publication of her paper, and it is the purpose of the present discussion to align these more recent facts with the older in a schematic series based upon her suggestions. The life cycles of species representing the salient positions in the series are illustrated in the accompanying diagrams and include the facts gained from my recent study of chromosome arrangement in somatic nuclei of *Yucca rupicola* Scheele. (See text fig. 1.)

As Clemens Müller (1909) showed for *Yucca aloifolia*, *Y. draconis*, and *Y. guatemalensis*, the nuclei in root tips of *Y. rupicola* also contain a com-

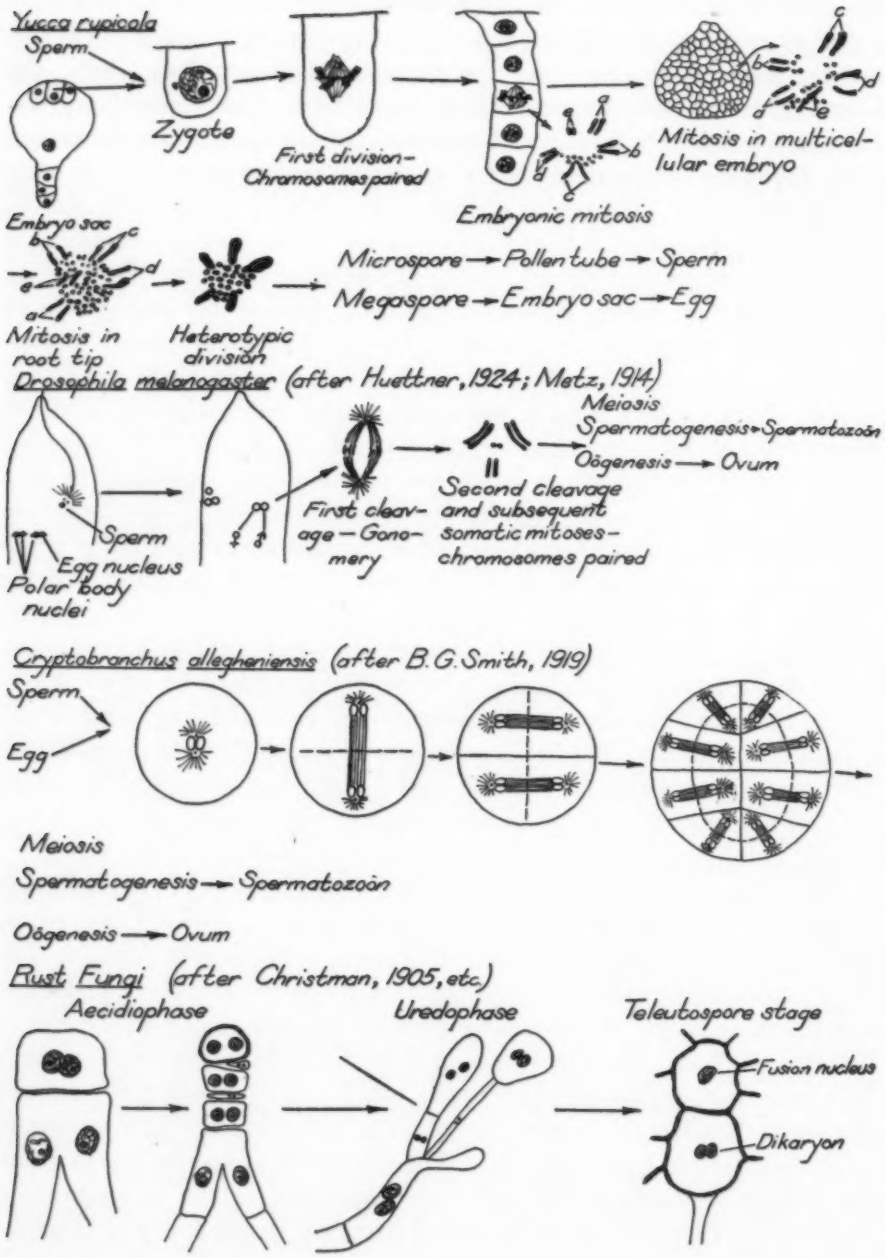

Fig. 1. The life cycles of several organisms, illustrating the variations in the behavior of gametic chromatin after syngamy.

bination of both long and short chromosomes (the diploid number in *Y. rupicola* is sixty, of which ten are large and fifty small), which are arranged in pairs upon the equatorial plates of all somatic mitoses studied —in root tips, in ovarian cells, and in cells of young embryos, including the equatorial plate of the first division of the zygote. These data indicate that the homologous chromosomes become associated in pairs during or immediately after karyogamy, appear thus upon the equatorial plate of the first embryonic division spindle, and continue to occur in this paired relation in each equatorial plate stage throughout the entire diploid phase. A study of the meiotic prophases of *Y. rupicola* seems to indicate that the culmination of this condition is a typical chromosome conjugation in synapsis similar to that described for *Lilium* (C. E. Allen, 1905).

For *Yucca* the three phases of fertilization which have been recognized above—plasmogamy, karyogamy, and pairing of homologous chromosomes—appear as essentially a single process. So far as I find from the literature it is the only organism in which cell fusion is followed so promptly by chromosome pairing. It stands as one extreme in such a series as is above set forth.

Huettner (1924) reports for *Drosophila melanogaster* that, following the coming together of the gametic pronuclei in the resting condition, the chromosomes appear in two gonomeric groups side by side on separate spindles at the first cleavage division. On the second division spindles the evidences of gonomeric separation have completely disappeared, and the homologous chromosomes are closely paired. Huettner (1923) and Metz (1914, 1916) had previously shown that this paired condition persists throughout the remainder of the diploid development of *Drosophila*. The gonomeric independence of the parental germ plasms in the first cleavage gives way to the perfect chromosome pairing of the second division. Such sharp transitions are not provided for in current theories of nuclear and chromosomal activities.

The persistence of the paired arrangement throughout almost the entire diploid phase, as well as the almost diagrammatic perfection of the pairing found in a large number of dipteran species, as reported and figured by Metz, are sufficient grounds for assuming that *Drosophila* and other similar forms occupy the next position in a series based on the time at which chromosome pairing appears.

Next perhaps, for the present, may be placed the great majority of plant and animal species, since in most forms plasmogamy and karyogamy are both accomplished as the ordinary type of syngamy, but chromosome pairing, as reported at least, does not occur before synapsis in the meiotic prophases. Several factors should be considered in connection with the

massing of all these forms into a single group. In the first place the number of authors who have considered chromosomes from the standpoint of pairing in somatic divisions is relatively small, and many cases in which the tendency to pair is exhibited have probably been overlooked or ignored by investigators who were primarily concerned with other problems. Also it is a noteworthy fact that the majority of species in which pairing in somatic nuclei has been observed are characterized by relatively long, rod-shaped chromosomes. In *Yucca*, with its complement of a mixture of long and very short chromosomes, Müller (1909) noted that the pairing is more evident in the rod-shaped than in the very short chromosomes, and my results with *Y. rupicola* confirm this. The large chromosomes in the nuclei of *Yucca* are much less numerous than the small ones; doubtless the visible evidence of pairing in somatic nuclei is inversely proportional to chromosome number. The literature on these various points is to a certain extent conflicting. Thus, while such long chromosome forms as *Galtonia candicans*, *Pisum sativum*, *Eucomis bicolor*, *Hyacinthus orientalis*, *Chionodoxa lucillae*, and many others have been described (Strasburger, 1905, 1907; Müller, 1909, 1912) as showing pairing in the somatic mitoses, in many other forms, also having relatively long chromosomes, such as species of *Allium*, *Lilium*, *Trillium*, *Vicia*, *Podophyllum*, *Crepis*, etc., the chromosomes have been frequently figured and described by various authors with no reference to a possible paired arrangement during these stages. Furthermore, for the somatic nuclei of *Spinacia oleracea* (Stomps, 1910) and *Mouriria anomala* (Ruys, 1924), in which the chromosomes are figured as quite short, close pairing has been described. The relation between chromosome number and recognizable pairing is certainly not rigid, since there are many species with few chromosomes, such as *Crepis capillaris* (2n = 6), in which the diploid sets are usually figured with little evidence of pairing. In *Beschorneria superba* (2n = ca. 50), on the other hand, Müller (1912) recognized marked chromosome pairing.

In a few species of plants and animals the individuality of the parental chromatin complexes is maintained for a brief period after plasmogamy has taken place. Gonomery is reported for the first division of the embryo of *Pinus* by Miss Ferguson (1904). In species of *Cyclops* Rückert (1895) and Häcker (1895) have demonstrated the persistence of parental chromatin groups in the form of double nuclei which occur in all cells up to the eight-celled stage. According to Rückert for *C. strenuus*, all the cells of the thirty-two-celled embryo are binucleate. In later embryonic stages some of the cells are uninucleate as a result of karyogamy, but a few binucleate cells can be observed as late in the larval development as the time of formation of the three pairs of nauplius extremities. For *Crypto-*

branchus B. G. Smith (1919) has reported a condition of gonomery which persists through four successive cleavage divisions in the development of the embryo. Evidences of the individuality of the parental nuclear elements were seen in some nuclei in the gastrula stages. These forms stand intermediate in the series, since in them the process of plasmogamy initiates the diploid phase, karyogamy occurs sometime later in embryonic development, and so far as is reported, pairing of the chromosomes becomes recognizable only in the prophases of the reduction divisions. All three so-called phases of fertilization are well separated.

Various species of fungi represent the other extreme of such a series. Within this group the nuclear conditions are very diverse and frequently as yet imperfectly understood, but the nuclear phenomena in the Uredinales furnish an example of the greatest possible separation between plasmogamy and karyogamy. As mentioned above, the diploid phase is initiated by nuclear migrations or cellular fusions among the subaecidial hyphae (Blackman, 1904; Christman, 1905), or by fusions of spermatia with receptive hyphae somewhat prior to the formation of the aecidia (R. F. Allen, 1930, 1932, 1933; Andrus, 1931). Nuclear fusion does not follow immediately, however, and the rust goes through a long and profuse dikaryonic development. The uredospores are binucleate and the dikaryophase ends only with the maturing of the teleutospores. These are the so-called zeugites, and in them karyogamy occurs (Poirault and Raciborski, 1895; Sapin-Trouffy, 1896), only to be followed immediately by meiosis, which brings about the haploid condition in connection with the production of the promycelium and the sporidia.

From the cases of gonomery reported by Rückert, Häcker, B. G. Smith, and others it is seen that the union of parental nuclei may be a very gradual process, that they do not approach each other and, as two drops of water, suddenly plunge together because of surface tension forces. The approach and fusion of nuclei in *Cyclops*, for example, extends through several mitotic generations, the association gradually becoming more intimate until at last the dual structure of the nuclear mass in each cell is detectable only in interkinesis by the presence of a very slight median constriction or a very faint partitioning membrane between the homologous halves. In the well-known case of the rusts the union of parental nuclei is not at all necessary for the development of the sporophyte. Through countless mitotic generations the nuclei persist as separate entities. In the light of the recent evidence presented by Heitz and Bauer and Painter for the widespread possibility of synapsis in diploid somatic nuclei the extreme nuclear conditions exhibited by *Yucca* and some of the Diptera on the one hand, and by many of the Uredinales on the other,

as well as all the known intermediate conditions, must certainly be taken into account as a possible vehicle for many varying types of hereditary phenomena.

My sincere thanks are due to Professor R. A. Harper and Professor J. S. Karling for many valuable suggestions given me during this study.

SUMMARY

1. The composite results of many investigations on the nature of the sexual process in plants and animals indicate that in general three definite phases are to be distinguished, namely, fusion of protoplasts as wholes (plasmogamy), fusion of gametic nuclei (karyogamy), and pairing of the homologous chromosomes.

2. From the standpoint of its effect on inheritance the last-named phase, the pairing of homologous chromosomes, has been greatly emphasized.

3. Different organisms vary strikingly in the interrelationships of the three phases of fertilization. *Yucca* shows chromosome pairing immediately after karyogamy, at the beginning of the diploid phase, and species of the Uredinales undergo karyogamy only at the end of the sporophytic development. These are extreme conditions and such forms as *Drosophila*, *Lilium*, *Pinus*, and *Cyclops* stand intermediate in the series.

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Notes on Texas phloxes

EULA WHITEHOUSE

A study of several hundred specimens from the large eastern herbaria and many more from Texas field and herbaria sources has brought to light a number of interesting facts in relation to the annual phloxes. Those who have studied the annual phloxes in their native habitat have long felt the need of a study which would bring into harmony descriptions and field specimens.

Five annual species of *Phlox* have been described as natives of Texas. The first of these was *Phlox Drummondii*, described by Hooker (1835) from seed sent by Thomas Drummond. Gray (1870) recognized two varieties of *Phlox Drummondii*, *villosissima* and *tenuis*, but later (1886) notes that *tenuis* is "seemingly very distinct." This classification was maintained by Coulter (1892), but subsequently Nelson (1899) gave specific rank to *tenuis* and Small (1903) to *villosissima*. Brand (1907), in his monograph of the genus *Phlox*, adds to the confusion by reducing *P. tenuis* and *P. villosissima* to varieties of the subspecies, *eu-drummondii*, of *Phlox Drummondii* and adding a new subspecies, *glabriflora*. *Phlox roemeriana* was described by Scheele (1848) from specimens carried back to Germany by Roemer. Nelson (1899) added *P. aspera* to the list of annuals, but suggested that it might possibly prove to be a perennial. Brand recognized *Phlox roemeriana*, but considered *P. aspera* as a variety of *P. Drummondii*.

Of these five species, *P. Drummondii*, *P. tenuis*, and *P. roemeriana* are undoubtedly distinct species and will be discussed in a later article. *Phlox aspera* Nels. is considered by Wherry (1930) to be a perennial, which he classes as a variety of *P. pilosa* L. The status of *P. pilosa* as exemplified by Texas specimens needs further study, for a great range of variability is shown by specimens assigned to this species. The present study has shown that *P. villosissima* (Gray) Small should be placed in the perennial group, closely related to *Phlox pilosa* L.

Phlox villosissima (Gray) Small is based upon Wright's specimen 1656 from the "pebbly bars of the Nueces River, S. Texas." The type at Gray Herbarium, as well as cotypes at Gray and Field Herbaria, clearly shows perennial characteristics. The label on the type bears the inscription, "*Phlox Drummondii*, Hook. var. *viscosissima*, Gray." The thick, glutinous leaves make "viscosissima" as appropriate a name as "villosissima." Only a few specimens have been found showing the characteristics of Wright's type specimen. Further study may reduce it to an ecological form, for it grows in an unusual environment for a phlox.

The confusion which has arisen in the determination of phloxes from

Southern Texas has resulted from this description of *P. villosissima* as an annual, an error easily accounted for by the absence of lower leaves from the type and the close resemblance of its long woody tap-root to an annual root. Another cause is the distribution of Heller's specimen 1435, collected on Nueces Bay in 1894 and incorrectly determined and distributed as *P. Drummondii villosissima* Gray. This classification was followed by Brand (1907), but Nelson (1899) thus assigns it doubtfully.

As Wright's specimen stated that it was found on pebbly bars, the writer, in trying to re-locate the type locality followed the suggestion of Dr. B. C. Tharp to look in the vicinity of Uvalde, where the Nueces River cuts through the southwestern edge of the Edward's Plateau and where bars of chalky gravel are numerous in the wide bed of the river. Numerous plants which closely matched the type were found at two crossings of the Nueces near Uvalde. A fruitless search was made on the lower course of the river, where the channel narrows and deepens and there are no gravel bars.

The unusual habitat of this phlox is worthy of special note. The gravel in which the scattered plants are found is unusually coarse and sometimes quite deep, so that the long woody perennial roots on some plants extend three or more feet. The plants are afforded some shade in morning or evening from scattered trees or shrubs several feet away.

The pubescence of different plants collected at the two crossings varied considerably, being very dense on some and scant on others. Plants on the Medina River growing on a shady bank in rich humus are even less pubescent and viscid and grow much taller.

Specimens examined which check carefully with the type are as follows:

Texas: Without definite locality—Wright 1656 (G, F), Lindheimer 467 (ANS), Bigelow (F), Pope (G); Sutton County—Sonora, Jones 1013801 (M); Pecos County—Sheffield, Jones 28281 (M); Val Verde County—on Devil's River, Orcutt 6059 (M); Real County—Leaky Tharp (T); Uvalde County—Laguna to Brackettsville on W. Nueces R., Whitehouse (T), sw. of Uvalde, Whitehouse (T). A densely villous specimen of *Phlox pilosa* L. from Granite, Greer County, Oklahoma, needs further study. With the exception of this and Bigelow's specimen, the range of *Phlox villosissima* seems to be confined to the streams of the limestone hills of Central and Southwestern Texas.

In the vicinity of Nueces Bay, the phlox distributed by Heller grows very abundantly in sandy wooded regions. Its relationships need further study, being intermediate between *Phlox Drummondii* Hook. and the plant so abundant on the sandy prairies south of the Nueces River, which Brand has called subspecies *glabriflora* of *Phlox Drummondii*.

Careful field and herbarium study has convinced the writer that this southern annual *Phlox* is worthy of specific rank. It grows abundantly on sandy prairies south to Raymondville, Willacy County and westward to the southern parts of Duval and Webb Counties. Except on boundary lines, these plants show little variation and agree quite closely with Brand's characters of a branched habit, glabrous corolla tube and lanceolate leaves.

Brand cites as specimens of this subspecies *glabriflora* Wright 1656 and Berlandier 2526 (Herb. DC), not giving the herbarium in which the Wright specimen belongs. This admits of some confusion, as Wright 1656 (Gray Herbarium) is the type of *Phlox villosissima*. Another specimen collected by Wright and distributed as 1656 is *Phlox roemeriana* Scheele. The fact that Wright's route across Southwestern Texas lay about a hundred miles northwest of the present known western limit of *Phlox glabriflora* suggests that the specimen which Brand cites may have been erroneously attributed to Wright. However, a few specimens collected by Small and Wherry 11803 (NY) near Orange, Apr. 11, 1925, are much further out of range. Brand undoubtedly errs in giving New Mexico as the type locality of Wright's specimen, for no annual phloxes are found west of the Pecos River. Judging from other specimens collected by Wright, the number would indicate that it came from the region between San Antonio and Del Rio.

A number of specimens of Berlandier's collection 2526 represented in our eastern herbaria have been examined. Berlandier's notes indicate that he was familiar with the plant throughout the region where it is most abundant. The specimen at Philadelphia bears the notation, "fl. violacei. in locis arenosis. De Matamoras a las Nueces April, 1834." At Gray Herbarium and Missouri Botanical Garden the label is the same except for the locality which reads, "Del Arroyo Colorado al Rio de las Nueces." These and other specimens without data (ANS, F) all show the characteristics noted by Brand.

Few variations have been observed in *Phlox glabriflora*. The flowers do not have the "phlox-purple" color of some of the other annuals, but are paler, the color varying from pink to lavender and fading blue. White flowers have been noted at Redfish Bay by Dr. Tharp. The flowers when pressed usually show a bluish color along the margins of the lobes. The plants from Redfish Bay likewise vary in having a very short style and some have almost eglandular pubescence. In older plants showing long continued branching, the leaves have a tendency to become broader and shorter, but still remain lanceolate in shape.

Phlox glabriflora is markedly different from the other annual species of *Phlox* which have been described, but is more closely allied to *Phlox*

Drummondii Hook. than to *Phlox tenuis* (Gray) Nelson or *Phlox roemeriana* Scheele. It varies from the former in its short, glabrous corolla tube, its thin, narrow, lanceolate, non-viscid leaves, its flattened calyx lobe tipped with a short callous point, and its widely branched habit.

Phlox glabriflora (Brand) Whitehouse, n. comb.

Phlox Drummondii Hook. subspecies *glabriflora* Brand in Engler's Das Pflanzenreich IV. 250: 71. 1907.

ROOT: annual, a long primary from which, in widely branched plants, arise two large branches 3–5 cm. below the soil surface. STEM: central 15–30 cm. long, erect, pubescent above with long, soft, mostly eglandular hairs and almost glabrous below, the mid-portion larger than the slender base; basal branches numerous, opposite, glabrous and slender below, decumbent-ascending; upper branches 2–3 alternate, slightly pubescent; basal internodes very short, 1–5 mm., the upper increasingly longer, 1–2 cm. LEAVES: lower linear-lanceolate with narrowed bases, longest at the third and fourth nodes, 6½ cm. long and 2½ mm. wide, thin and almost glabrous; upper lanceolate-acuminate, base narrowed to rounded, but scarcely clasping, alternate, pubescent with a few soft scattered hairs; bracts lanceolate-acuminate, 10–15 mm. long; branch leaves linear-lanceolate, often ensiform, 2–4 cm. long. INFLORESCENCE: loosely cymose, the peduncles commonly 4–5-flowered, 2–4 cm. long, stout; terminal flower pedicel 5 mm. long or less, the axillary pedicels much longer, stout. CALYX: 9–10 mm. long, the lobes slightly longer than the tube, pubescent with numerous long, slender hairs, eglandular or tipped by small glands, mid-nerve conspicuous even in flower, extending visibly about ¾ length of the calyx and giving a keeled effect to the calyx tube, the two lateral nerves being visible only about ½ the length; lobes linear, flattened, slightly thickened with a short acute callous tip, spreading or recurved in flower, but erect in fruit. COROLLA: tube pale pink, glabrous, with a broad base showing a sharp constriction 2 mm. up, 10–15 mm. long but commonly 13 mm., the upper stamen attached near the apex of the tube, inner basal hairs inconspicuous; lobes obovate to cuneate, apex acute or rounded, 9 mm. long and 8 mm. wide, lavender, sometimes pink, white or blue, mid-vein darker and two conspicuous oblong white spots near the base; throat white, slightly funnel-shaped, 2–3 mm. broad. PISTIL: about 3½ mm. long, enclosed in the minute, greenish disc; stigmas linear, 1¼ mm. long; style narrow, ½–1 mm. long; ovary ovoid, 1¼ mm. long, carpels 1-ovuled. CAPSULE: ovoid, 5–6 mm. high. SEED: 3, light gray, elliptical-oval, 3×1½ mm., not winged, shallowly rugose.

Phlox glabriflora (Brand) Whitehouse. n. comb.

(*Phlox Drummondii* subspecies *glabriflora* Brand.)

Caulis herbaceus, ramosus, superior hirsutis longis mollissimis pubescens et inferior glabrus. Folia infima petiolata linearia-lanceolata, opposita, glabra, 6½ cm.×2½ mm.; media alternata, sessilia lanceolata-linearia; summa e basi

latiori lanceolata. Rami oppositi e basi, multi. Pedunculi 2–4 cm. longus, validi. Calyx 9–10 mm. altus, hirsutus, laciniae lineares tubo paulum longiores, abrupte apiculatus. Corolla lilacina, tubus 13 mm. longus, glabrus, limbi laciniae obovatae vel cuneatae, 9–10 mm. longus, albae circum oculum. Ovarium ovatum, loculis 1-ovulatis. Capsula 5–6 mm. alta.

Distribution: Nueces County to Willacy and Webb Counties, abundant; Orange County, rare; from the Nueces River to the Medina River, rare.

Specimens examined:

Brooks County—near Falfurrias, April 6, 1931, McKelvey 1745 (US); March 6, 1934 and July 16, 1925, Tharp (US, T); July 17, 1930, Wolff 2419 (US); March 17, 1934, Whitehouse (T); Cameron County—May 10, 1900, Bailey 247 (US); March 20, 1908, York (US, T); Jim Hogg County—Hebbronville, Feb. 13, 1919, Hanson 343 (G, US, T); March 15, 1931 and March 5, 1934, Tharp (US, T); March 17, 1934, Whitehouse (T); Kennedy County—Sarita, Apr. 11, 1905, Lewton 124 (ANS, US); Feb. 1829, Berlandier 532 (ANS); Kleberg County—Riviera, Feb. 23, 1931, Harrison (US); March 15, 1931, Tharp (T); March 17, 1934, Whitehouse (T); Nueces County—Mustang Island, April 16, 1933, Whitehouse (T); Orange County, April 11, 1925, Small and Wherry 11803 (NY); Webb County, March 5, 1934, Tharp (T); Willacy County—Redfish Bay, March 5, 1934, Tharp (T); between Nueces and Medina Rivers, Jan. 1853, Thurber (G); without definite locality, Apr. 1834, Berlandier 2526 (ANS, F, G, M).

The preceding list includes only the forms with a glabrous corolla tube. Along the boundaries, various forms with pubescent corolla tubes show evidence of hybridization and these will not be reported without further investigation. The specimens listed from Cameron County were probably collected in the northern part which has since been cut off into Willacy County.

Grateful acknowledgment is made to Dr. B. C. Tharp for his plant collections, assistance in borrowing material, and especially for his field work in 1931 and 1934 in checking the distribution of the annual phloxes. Appreciation is also extended to the curators of the various herbaria who have assisted with the loan of material. The following list includes the herbaria from which specimens were borrowed and the abbreviations used in referring to them:

ANS—The Academy of Natural Sciences of Philadelphia.
B—Brooklyn Botanical Garden.
F—Field Museum of Natural History.

G—Gray Herbarium of Harvard University.
M—Missouri Botanical Garden.
NY—New York Botanical Garden.
NT—North Texas State Teacher's College.
US—United States National Herbarium.
T—University of Texas Herbarium.

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Observations and experiments on sex in plants[1]

JOHN H. SCHAFFNER

Because of the complexity and diversity of sexual phenomena in the plant kingdom, many points having a bearing on the theory of sex are still obscure and many who deal with the subject are apparently unacquainted with this complexity and with the homologies and inter-relations of the various categories of sex conditions and structures. Whatever may be the basis for the various hypotheses of sex in *Drosophila* and other advanced animal species with rather constant individual sex conditions these hypotheses can refer to only a very small fraction of the sex conditions present in both plants and animals and are not to be applied as generalizations, as many under the spell of the *Drosophila* obsession are inclined to do.

The following observations and experiments on sex expression in various plants in relation to heredity and environment give further evidence on the nature of sexuality and sex as physiological phenomena. Apparently many of those who deal with the problem of sex are unacquainted with the homologies and differences existing between the sexual conditions and structures of the gametophytes and sporophytes of higher plants. It is an absolutely established fact that the maleness or femaleness of the gametophytes of the heterosporous plants never depends in any way on the segregation of hereditary factors nor even in the slightest degree on an allosome differential which may be present after the reduction division. The unisexuality of the gametophyte of heterosporous plants is always determined by the physiological, sexual state of the tissue from which the sporocytes and spores are derived, whether the sporophytes are monosporangiate or bisporangiate, whether they contain allosomes or not. It must be emphasized that there is never any segregation of chromosomes or genes in the heterosporous plants which has any influence whatever in determining the gametophytic sex conditions. This fact is in itself a proof that sex determination is primarily physiological. In view of this condition of things, it is remarkable that many genetecists still seem to think that the unisexuality of the sporophyte must be brought about by a fundamentally different biological process, namely by some hereditary differential. But most sporophytes are hermaphrodites in respect to sex condition and in both the monecious plants and those with bisporangiate flowers the sex of the given part or tissue is determined by physiological states. It is also well to remember

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that the unisexual gametophytes of heterosporous plants not only show the most extreme sex dimorphism but also the greatest stability of their sexual states of any organisms whether plant or animal. It is in the unisexual sporophytes where sex reversal is often easily accomplished. In those cases where allosomes are present the male gametophytes which contain the "female determining" chromosome retain a constant male state and produce spermatozoids without exception as definitely as their brother male gametophytes do which contain the "male determining" chromosomes. It seems reasonable to demand that those who deal with such a fundamental potentiality as sexuality be acquainted with as much plant morphology at least as is now usually taught in the general elementary botanical course.

CHANGE OF SEX CONDITIONS IN THALICTRUM DASYCARPUM FISCH. AND LALL.

In 1919, the writer published some observations on the nature of the diecious condition in *Thalictrum dasycarpum* and in 1923, he published evidence of definite sex reversal in both directions in this species and also evidence of instability in *Thalictrum dioicum* L. In 1925, the results of further experiments on these two species were published, establishing the fact that the sexual condition can be changed from year to year. In the meantime, Kuhn has made extensive observations on a number of species, studying the chromosome conditions and carrying on breeding and hybridization experiments. All of these studies go to show that *Thalictrum* is a very suitable genus for the study of dieciousness and sex conditions in general.

In 1931, the writer began a new series of observations and experiments on *Thalictrum dasycarpum* in order to determine more definitely the stability or instability of the individuals in respect to their sexual expression. The genus *Thalictrum* belongs to a family near the base of the dicotyls and exhibits, as numerous other genera both low and high in the phylogenetic scale, a rather close gradation of species from those with typical bisporangiate flowers with no indication of a diecious nature to species which are strongly diecious both in the distinctness of the sex individuals and the constancy of the given male and female conditions. *Thalictrum* is interesting among diecious angiosperms in that no vestiges of the opposite sporophylls are present, the sporophylls all developing as normal stamens and carpels except in the special cases of sex-reversal of individual flowers when the sporophylls may be of any degree of perfection or imperfection. This flower condition corresponds to the monecious and diecious flowers of the gymnosperms where usually no opposite sporophyll vestiges are present except in the highly specialized Gneteae.

A study of the sex expression of the various branches on the same shoot of intermediate plants was made and these differences, as will appear below, correspond to the differences between entire annual shoots from the same crown or the differences which may develop from year to year. Out of a large number of carpellate shoots, gathered from their native habitats, studied statistically a few representative examples are presented below. Shoot No. 1 had ten branches with pure carpellate flowers and one branch had one flower with stamens among many pure carpellate flowers. No. 2 had one branch with pure carpellate flowers and five branches each with one flower containing stamens among the carpellate flowers. No. 3 had twelve branches with all pure carpellate flowers and five branches had each one flower with stamens among the carpellate flowers. No. 4 had four branches with all pure carpellate flowers, five branches each with one flower with stamens, one branch with three flowers with stamens, and one branch with four flowers with stamens among the carpellate flowers. No. 5 had four branches with all pure carpellate flowers, four branches each with one flower with stamens, one branch with three flowers with stamens, one branch with four flowers with stamens, two branches each with five flowers with stamens, one branch with six flowers with stamens, and one branch with seven flowers with stamens, among the carpellate flowers. No. 7 had one branch with all pure carpellate flowers, three branches each with one flower with stamens, seven branches each with two flowers with stamens, one branch with eight flowers with stamens, two branches each with nine flowers with stamens, and one branch with ten flowers with stamens among the carpellate flowers. No. 10 had two branches with all pure carpellate flowers, one branch with one flower with stamens, two branches each with two flowers with stamens, two branches each with three flowers with stamens, two branches each with four flowers with stamens, one branch with five flowers with stamens, one branch with six flowers with stamens, one branch with seven flowers with stamens, one branch with eleven flowers with stamens, one branch with twelve flowers with stamens, and one branch with sixteen flowers with stamens among the carpellate flowers.

In Northern Minnesota an interesting intermediate plant was found, in 1934, in which all the flowers were typically bisporangiate with the stamens below and the carpels above. Just beside this plant were some individuals with slight sex reversal and some pure carpellate and staminate plants.

In 1931 also, thirteen plants were transplanted from their native habitat of partly shaded, rich, alluvial soil to an exposed, rather sterile and rocky, clay soil. These plants had the following sex expressions in 1931.

Nos. 1 and 2 were of mixed sex expression; decidedly carpellate with some staminate development.

No. 3. Mixed sex expression; staminate with some carpel development.

Nos. 4, 5, 6, pure carpellate.

Nos. 7, 8, 9, 10, 11, 12, 13, pure staminate.

The plants developed no flowers in 1932 but made a good growth. In 1933 the flower development was as follows:

Plant No. 1 remained decidedly carpellate, but with some bisporangiate flowers, each with one to several stamens.

Plant No. 2, had three shoots. The first and largest was pure carpellate in expression, the second had nearly all the flowers bisporangiate, while the third was prevailing carpellate but with numerous flowers showing one or more good stamens.

No. 3 had six shoots all decidedly staminate but each had several flowers with some carpels.

No. 4 had two shoots strongly carpellate and each had a flower with one good stamen and a second flower with an imperfectly developed stamen.

No. 5 was strongly carpellate but each of its three shoots had several flowers with one or more good stamens.

No. 6 had two shoots, both pure carpellate.

No. 7 had six shoots; three shoots had each several flowers with one or two good carpels among the staminate flowers; one flower had three good carpels; the other three shoots of this plant were all pure staminate.

No. 8 had several flowers with one carpel each.

Nos. 9, 10 and 11 were pure staminate.

No. 12 had a great number of typical staminate flowers and several flowers with one or two imperfectly developed carpels; one flower had one good carpel.

No. 13 was prevailingly staminate but with a considerable number of bisporangiate flowers each with one or more good carpels.

Thus in two years after a change in habitat, of the three originally pure carpellate plants two developed some maleness and one remained pure female; and of the seven plants originally pure staminate four showed some reversal to femaleness and three continued pure male expression.

Since the ground was very sterile, the plants received an application of manure in 1933. This increased the vigor of growth decidedly but apparently had no special effect on the subsequent sex expression. In 1934, the thirteen individuals had the following sex conditions:

Plant No. 1 was small and did not bloom.

Plant No. 2 had seven flowering shoots; one shoot had a mixture of

pure staminate, pure carpellate, and bisporangiate flowers, the latter ranging all the way from having one member of the opposite sex to flowers with about an equal number of stamens and carpels; one shoot was mostly carpellate but had one stamen; the other five shoots had all pure carpellate flowers.

No. 3 had three flowering shoots; two shoots were staminate with some carpel development; the other shoot, which was the largest, was decidedly carpellate with numerous pure carpellate flowers but with some bisporangiate flowers and two pure staminate flowers.

No. 4 had developed four flowering shoots; one was carpellate but had one bisporangiate flower with one good pollen-producing stamen; the second was carpellate but with three bisporangiate flowers, each with one good pollen-producing stamen; the third shoot was also prevailingly carpellate but with two bisporangiate flowers each with one stamen and one of them with a carpel-stamen mosaic additional; the fourth shoot, which was the smallest, was pure carpellate.

No. 5 had two flowering shoots, both pure carpellate.

No. 6 had two flowering shoots, the one was pure carpellate and the other was carpellate but with one flower with an imperfectly developed stamen.

No. 7 had nine flowering shoots; two shoots had only pure staminate flowers; four shoots had some pure staminate flowers and each of them also had a number of decidedly carpellate flowers but with one or more stamens; the seventh shoot was decidedly carpellate, about half of the flowers having one or more carpels, the eighth shoot was extremely carpellate, developing more carpels than stamens, with only four pure staminate flowers among over 100 carpellate ones which produced good seed; the ninth shoot was small and produced about as many stamens as carpels mostly in bisporangiate flowers.

No. 8 had six shoots, five of which were pure staminate and one with mixed sex expression, having thirty pure staminate flowers, sixteen bisporangiate flowers with 1–12 carpels each and one pure carpellate flower.

No. 9 had four flowering shoots all pure staminate.

No. 10 had three flowering shoots all pure staminate.

No. 11 had five flowering shoots, four pure staminate, and one staminate but with two flowers each with an imperfectly developed carpel.

No. 12 had five flowering shoots all pure staminate.

No. 13 had four flowering shoots of which three were pure staminate and one was staminate but with a flower containing an imperfectly developed carpel.

From the above record, it appears that there is the same diversity in

sex expression in individual plants from year to year and in the individual annual shoots developed from the same plant as there is between the main branches of a single bisporangiate shoot, as determined by statistical methods on plants growing in their original habitats.

Of the three originally pure carpellate plants (Nos. 4, 5, 6,) all changed to intermediate sex expression altho one showed only the slightest trace of sex reversal. Plant No. 4 developed some stamens in both 1933 and 1934. Plant No. 5 showed mixed expression in 1933 but was pure female again in 1934. Plant No. 6 remained pure female in 1933 but developed a single imperfect stamen in 1934. Thus all three showed the presence of both male and female potentiality altho in general the expression was decidedly female. Of the seven originally pure staminate plants (Nos. 7, 8, 9, 10, 11, 12, 13,), five showed some reversal to femaleness and two remained pure male for the period of four years. Of the three originally bisporangiate plants (Nos. 1, 2, 3), No. 1 remained practically unchanged, continuing a carpellate-staminate sex expression. Plant No. 2 showed decided sex disturbances, producing a pure carpellate shoot in 1933 along with 2 bisporangiate shoots. Plant No. 3, which was originally staminate-carpellate with a preponderance of staminate expression remained about the same in 1933, while in 1934, of its three developed shoots, two were decidedly staminate and one was decidedly carpellate. It had changed from a predominantly male reaction to a predominantly female reaction. The most decided change in sex reaction was shown by plant No. 7 which changed progressively from a pure male reaction to a decidedly female reaction with hundreds of good fruits in 1934. (Fig. 1)

As a result of these observations it is evident that in a diecious plant like *Thalictrum dasycarpum*, every cell has a bisexual potentiality as the writer and others have maintained and as Kuhn has recently stated. The hereditary factors which cause dieciousness are not a set of male and female segregating and aggregating genes, but rather an accumulation of new potentialities in the protoplast with an originally bisporangiate potentiality. These potentialities, with a given internal or external condition, cause a physiological balance in the egg or zygote, or in the vegetative cells, before, at the time of, or after fertilization, of such a nature that the sex balance swings, for the time being, toward female (+) or male (−). Furthermore, there are potentialities evolved, in passing from the bisporangiate flower condition to the diecious state, which determine or condition both the degree of intensity and fixity of the sex differentation. It has been found from a taxonomic study that the presence or absence of vestiges of the opposite sporophylls in a flower are no criterion for determining the fixity of the sexual states. These physiological potentialities,

in *Thalictrum* and a great number of other genera, form a closely graded orthogenetic series, giving a large number of types of dieciousness in respect to the fixity of the male and female states and the percentage of intermediates or bisporangiate individuals usually appearing in their native habitats.

URTICASTRUM DIVARICATUM (L.) KTZ.

Urticastrum divaricatum is a perennial, herbaceous, monecious species which usually grows from one to four feet tall. After attaining some size it begins to produce loose staminate flower clusters in the upper leaf axils and finally at the end of the growing period several carpellate flower clusters at the tip of the stem. The carpellate inflorescences are usually arranged in the form of a terminal rosette. After seed production the aerial shoots begin to die down to the ground. Some plants of this wood-nettle were dug up in the forest, in the autumn and planted in large flower pots in the greenhouse. After a period of rest they were brought into activity by means of continuous light and the new shoots soon made a vigorous growth. They were then allowed to grow and bloom normally and the usual sequence of axillary inflorescences appeared. The lower were staminate and at the tip of the stem a number of carpellate inflorescences developed. When well advanced in the blooming period they were vigorously treated for rejuvenation by means of continuous light (two 200 Watt Mazda bulbs) and abundant water. The shoots soon continued a vigorous new growth both in the terminal buds and in some lateral buds. The artificial light was turned off again and since it was now the last of March the plants were getting a continuously longer daily light period. In several weeks inflorescences began to develop and these were again staminate. Thus the normal gradient, which is first neutral, then male, then female, and finally death, was reversed to maleness again. Unfortunately these plants were injured by an attack of the red spider so that the tips were destroyed and the experiment was abandoned. With further development the vegetative axis would, no doubt, have produced carpellate inflorescences again at the culmination of the new gradient.

The sex determination in this plant is dependent on the functional state of the cells involved and this in turn is dependent on a definite gradient of maturity, which the given general hereditary constitution of the plant carries thru in a definite way in the usual ecological conditions in which it grows. In a new ecological world with rejuvenation of the terminal bud, a new reversed gradient in the reproductive condition is established and the sex balance swings from female to male rather than from male to female as in the original sequence. The sex expression does not

remain at the final female level but changes with the changed physiology of the cells concerned. This species is apparently a favorable monecious perennial for carrying on experiments in rejuvenation and the changing of the sex determination in relation to changing physiological states.

ZEA MAYS L. WITHOUT STAMENS

In 1928–30, the writer discovered a method by which the expression of maleness could be completely suppressed in Indian corn, resulting in pure female phenotypes. In a plot of "Narrow-grain Evergreen Sweet" corn planted on Oct. 10, 1928, there were 29 plants and not a single normal stamen was produced by the entire plot. This was such an interesting occurrence that it has been repeated several times since just for the pleasure of seeing the experiment come true. On Nov. 15, 1932 a small plot of "Woodburn Yellow Dent" corn was planted in the greenhouse, in a corner where there was shading of light because of the rafters in the roof. There was thus not only a decreasing photoperiod during the earlier stages of the growth of the plants but the light intensity was also decreased at various intervals of the day. The temperature was the ordinary variable greenhouse temperature and the plants were growing on shallow benches of good soil. The result was essentially the same in this dent corn as in the sweet variety. There were 12 plants in the plot and the terminal inflorescences and side ears were completely developed by March 10, 1933. There was not a stamen in the whole patch! Three plants had completely neutral, rudimentary "tassels" and nine plants had developed "tassels" with more or less female expression. In 1928 a plot of "Early Connecticut" dent corn representing a pure line, inbred for ten generations, had 44 plants. Of these, two plants produced a few stamens and 42 produced no stamens. In this case the photoperiodicity in combination with the temperature and other ecological conditions was not quite perfect, so that only about 95% developed with pure female reproductive expression.

In both monecious and diecious species there are various types of general hereditary constitutions which determine the constancy and direction of sex expression in relation to the ecological-physiological conditions. In *Zea mays* the hereditary balance is so conditioned that with the usual favorable environmental conditions of growth, the ecological light gradient causes the sex balance to swing from monecious expression to pure female expression or vice versa but not to pure male expression. In *Arisaema Dracontium* (L.) Schott. the situation is just the opposite, so that with favorable nutrition and abundant water the sex expression is completely monecious while with poor soil and dryness the expression is completely male. The sex-balance swings from moneciousness to maleness or

vice versa but rarely if ever to pure femaleness. In *Arisaema triphyllum* (L.) Torr. there is an equally balanced diecious condition so that the sex-balance swings from male thru moneciousness to female or from female thru moneciousness to male. In *Cannabis sativa* L. there is an equal sex-balance so that the change from femaleness to maleness or from maleness to femaleness is brought about with equal readiness and with this odd situation—exactly the same ecological conditioning with the proper photoperiod will cause the males to change to female and the females to male expression. In the diecious *Carica papaya* L., according to common report, apparently males change readily to females but females have, so far, not been changed to males.

It is evident that all hereditary complexes of the numerous common varieties of Indian corn can be induced, in proper environments, to undergo exactly similar sex reactions, no difference what the gene balance may be, and the similar reactions in respect to sex are initiated by environmental and not by hereditary conditions. Such a condition of things is contrary to Mendelian activity. As Yampolsky has recently stated: "The *n*-number of sex forms refuse to submit themselves to the concept that sex is an alternative kind of inheritance. Neither sex categories nor sex chromosomes hem in the variability of sex expression exhibited by *Mercurialis annua*." Richey and Sprague seem not to have understood the point which Yampolsky, the writer, and others have made when it was insisted that the diversity of sexual expressions does not correspond to a gene differential. The diversity of expression in the individual species or variety was always the point at issue. The main question is as to what causes various individuals of the same species or variety to have diverse sexual characteristics for the time being and what causes an individual to have different sexual expressions from year to year or from time to time. The attack has been and still is on the mistaken notion that there are allelomorphic male and female genes or determiners.

GENERAL DISCUSSION OF PROBLEMS RAISED BY THE EXPERIMENTS

With the acceptance of a physiological theory of sexuality and sex, and the abandonment of the sex gene hypothesis all the known morphological and physiological conditions of gametophytes and sporophytes and of hermaphroditism and unisexuality fall into a harmonious agreement. Some, however, still believe that the presence of allosomes points to a genetic explanation. But when we remember that all the fundamental characteristics of sexuality, even including unisexuality, were evolved before the appearance of segregative allosomes in the plant kingdom, it becomes much easier to believe that allosomes are the result of the evolution of

one kind of unisexuality rather than the cause. All we need to assume is a differential sex attraction in fertilization which would account for the fact that apparently the A and B allosomes have a definite relation to the two sexes as originally determined in the zygote. After sex reversal has taken place it is found that there is no such relation or rather that the relation is just the opposite from what it is in the original tissues.

Differential attractions, or compatibilities and incompatibilities are general phenomena, in both the plant and animal kingdoms, between gametes of like and unlike hereditary constitutions and are also in evidence in the differential synapsis of chromosomes and in the favorable or less favorable growth of pollen tubes in the ovules and carpels of seed plants. The physiological theory will also tolerate the assumption that some allosomes contain differential physiological factors, which set up differential physiological reactions at the time of fertilization and thus cause the sex balance to swing to the male or female state in the fertilized egg in the way that physiological states are initiated at a later period by ecological conditions and thru which the established sexual state may be completely reversed because the ecological influence is stronger than the assumed physiological determiners in the allosomes; or in the same way as sex is determined in the specific parts of bisporangiate sporophytes.

Diecious plants cannot be distributed into two distinct categories as subdiecious and true diecious, because there is often a close gradation series between the more primitive species with bisporangiate flowers thru various types of dieciousness to the extreme diecious condition. There is also a similar gradation series in the various types of monecious species and in the groups ranging from ordinary moneciousness to extreme dieciousness. The fact that some diecious species will readily change their sexual states in a given ecological condition while others do not has nothing to do directly with the *time* when the original determination took place. The intensity of the given physiological differentiation and its reversal are different phenomena from that which initiated the state in the first place and determined the dieciousness.

Correns' empirical formula for sex determination and inheritance, with its four general types of sex, its gene complexes, G, A, Z, and "Realizators" having varying valences, is only a fantastic thought pattern which does not at all agree with the known complexity and nature of the types of bisporangiate and diecious conditions present in the sporophyte of seed plants and the sex conditions shown by their gametophytes, nor the neuter conditions of the sporophytes of the homosporous plants and the various sex conditions of their gametophytes. The numerous ecological experiments on sex reversal in both monecious and diecious species as well as

the reversals accomplished in the lower types of gametophytes are all in agreement with the deductions to be made from an evolutionary and taxonomic study of plants and are also in accord with a correct genetic interpretation, namely when genetics is interpreted in terms not only of genes but also in terms of character expression thru the determination of physiological and ecological conditions and ontogenetic gradients.

The bisporangiate flowers also show a large number of types of hereditary expression, in respect to sex, comparable to the several types of monecious inflorescences. This is especially prominent in the lowest types of angiosperms with long floral axes. In the angiospermous bisporangiate flowers, if no disturbance, like dieciousness or moneciousness, has been introduced, the sex balance almost invariably proceeds from the neutral condition to the male condition to the female condition. Now in various species the growing bud may stay but a very short period in the male state and a long time in the female state so that the result is a flower with few stamens and very numerous carpels. Or the heredity may be just the opposite, giving a flower with many stamens and very few carpels. In other cases there are constantly as many stamens as carpels. Now these bisporangiate flowers are apparently much less subject to sex changes than either monecious or diecious types. The gradients seem to move at a very definite rate, altho in nature one occasionally finds a disturbance. It seems reasonable that the point of sex reversal on the floral axis might be shifted by employing suitable ecological conditions even tho the axis and time of its growth are very short when compared with the axes of the inflorescence of the monecious plants or the entire axis of a diecious species.

Sex determination is just as definite and just as decided in the more extreme types of monecious plants as in the diecious species, and constancy of the sexual states in the monecious branches and bisporangiate flowers is just as pronounced. Since we know that in the case of monecious plants, plants with bisporangiate flowers, and hermaphroditic gametophytes there is no shifting of chromosomes and no segregation of heredity, the physiological theory of sex determination is the only one to be entertained.

Some geneticists have been inclined to compare the universal sex dimorphisms and trimorphisms with specific dimorphisms arising in the ontogenetic development of an organism. Thus Emerson, in 1924, asked: "Is the association of pistils and stamens in a single flower either more or less mysterious than the differentiation of the aleurone layer from the rest of the endosperm?" This comparison however is beside the point. In a monecious plant the vegetative tissues in the respective male and female states,

as leaves and stems, show the same physiological differences as are shown by the stamens and carpels. But aleurone and non-aleurone layers have physiological and chemical differences not found in the leaves or stems of a corn plant. In sexuality we have male, female, and neuter conditions and these are general phenomena in the plant and animal kingdoms. But specific heredities due to Mendelian factors or more general potentialities are of an entirely different nature. An earthworm has both ovaries and spermaries in which ova and spermatozoa are produced and a stalk of corn also has ovaries and spermaries in which eggs and sperms are produced and these have the same general properties and reactions in either case. But an earthworm has neither endosperm nor aleurone layer.

Camp has recently shown by conclusive physiological-chemical tests that the male and female tissues of a monecious plant are just as definitely distinct as in a diecious species; and it must be remembered that in either case all the cells of a general male or female system show the given reaction and not merely the cells concerned directly with reproduction.

A fundamental theory of sex must then, among other things, take account of the evolution of the time of sex determination in the ontogenetic cycle as expressed in a given environment, the degree of intensity to which the given physiological state or reaction is developed at various stages of the ontogeny, also in relation to environment, and the readiness with which a given sexual state can be reversed from time to time in the life of the individual, whether it was originally determined in a vegetative tissue or in the zygote at the time of fertilization. We know from the action of haploid sporophytes and diploid gametophytes, when compared with their normal alternate generations, as diploid fern gametophytes for example, that the indications as to the nature of the hereditary units concerned are quite different in the gametophyte from what they are in the sporophyte in respect to sex as well as to other characters, altho they have in this case exactly the same chromosome complement and the same hereditary constitution.

SUMMARY

1. Both staminate and carpellate plants of the diecious *Thalictrum dasycarpum* underwent sex reversal in varying degrees when transplanted to a different habitat and the extent of the reversal was in some cases decidedly different in different years.

2. Shoots of the monecious *Urticastrum divaricatum*, after having produced the regular succession of staminate and carpellate inflorescences, on being rejuvenated by means of a continuous daily photoperiod, reversed from carpellate to staminate development.

3. A plot of "Woodburn Yellow Dent" *Zea Mays*, developed in the greenhouse with a short daily photoperiod and consisting of twelve individuals, showed only female development, there being a complete absence of stamens and normal male expression.

4. The experiments indicate that any sexual condition of an individual is not determined by Mendelian sex genes but by a physiological balance which is produced thru the interaction of the general hereditary potentialities of the cell on the one hand and the environmental conditions on the other. There are no sex genes as such and the gametophytes of heterosporous plants show that there are no sex producing or determining chromosomes, whether autosomes or allosomes, since the sex of the gametophytes and their gametes does not correspond to any special chromosome complement but always continues the condition previously determined in the gametophyte. The term "sex chromosome" is an extreme perversion of language and should not be tolerated.

5. The sexual conditions of the higher sporophytes may change from time to time in the individual and thus the sex present for the time is no criterion for determining the actual hereditary constitution in which the sex is being expressed: and it is evident from experimental data that all monecious and diecious species are finally amenable to sex changes thru the proper ecological influences.

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Fig. 1. *Thalictrum dasycarpum*. Abundantly fruiting shoot of plant which three years earlier was pure staminate.

Duplications in Zephyranthes

H. Harold Hume

Studies of plants placed in the genus *Zephyranthes* Herb., *Atamosco* Adans., have been made by Herbert (1837), Roemer (1847), Kunth (1847), and Baker (1888). These botanists discussed all species known to them at the times they wrote. Certain species now included in the genus were placed by Herbert, Roemer and Kunth in other genera. Holmberg (1905) wrote on *Zephyranthes* but limited his treatment of the genus to species, native and introduced, growing in Argentina. Since Baker's study of the group in which he described thirty-four species there has been no comprehensive examination of the genus and in the meantime about thirty plants believed to be specifically distinct have been added by various botanists. It is apparent that a careful comparative study of some of these additions has not been made. The necessity for such a study may be indicated by the fact that while the first listing of *Zephyranthes* in Index Kewensis (1894) gave fifty-one names that had been applied to supposedly different plants, only about fifty percent of them were regarded as valid. What was true of species included in the genus prior to that date is true in some measure of those added by description and publication subsequently.

How many of these may be identical with older species cannot be determined readily and a decision as to their exact status, in many instances, must await further study. While much may be determined by checking more recently described species against such herbarium specimens and illustrations of older described forms as are available, it may be pointed out that final dispositions must wait in some instances upon the examination of flowering plants in their native haunts or preferably upon comparative studies of living specimens grown under the same cultural conditions from seeds or bulbs of known origin. This is of course a difficult undertaking, but certain characters of these plants often are not presented satisfactorily in herbarium material and morphological characters cannot be determined readily without destroying specimens. Thus far a number of species have been studied from herbarium sheets, original descriptions, illustrations and living plants, and it has been determined that at least three duplications have been made. By the same method it has been found that a fourth species, dropped from the genus because it was regarded as a duplication, should be reinstated as proposed by Urban.

Z. citrina Baker and *Z. Eggersiana* Urb.

Baker (1882) described a yellow species, *Zephyranthes citrina*, and stated that his first knowledge of the plant had been gained from a speci-

men in flower furnished by Messrs. Veitch, Chelsea, England, and believed by them to have come from Demerara (British Guiana). The illustration accompanying Baker's description shows the tips of the spathe lacking. In this respect the drawing does not properly represent the plant and the description also is vague on this point. As a matter of fact, the spathe, as in other species, extends beyond the cylindrical portion and terminates normally in two points. The spathe is membranous in *Z. citrina* and quite apparently its upper portion was broken off or removed in some manner before the drawing was made. It also appears probable that this illustration represents two aspects of the same flower. Urban (1907) basing his conclusions upon specimens of a yellow-flowered plant collected in Cuba (Van Herman No. 803) and Haiti (Eggers No. 2634) described *Zephyranthes Eggersiana* n. sp., and referred particularly to the spathe characters presented by Baker as being different from those found in his species. After studying flowering plants produced from bulbs received from British Guiana, unnamed, and Trinidad, labeled *Z. Eggersiana*, an herbarium specimen collected by Van Herman (No. 803) and collections by others, the original descriptions, and the Baker illustration the conclusion is reached that *Z. Eggersiana* Urban is identical with *Z. citrina* Baker. It is difficult to say where this plant is native but with the knowledge now in hand it can be referred provisionally to British Guiana and possibly Trinidad. Juan T. Roig in a letter (now in the New York Botanical Garden Herbarium) to N. L. Britton expresses his belief that this plant is not native in Cuba.

Z. carinata Herb. and *Z. Tsouii* Hu

There grows in Mexico, a large pink-flowered plant that Herbert (1825) described as *Zephyranthes carinata*. Its native home is authenticated by specimens in various herbaria. It is widely distributed and cultivated as a garden plant in the warmer sections of the world. Recently, Hu (1927) described *Zephyranthes Tsouii* n. sp. from Chekiang Province, China. Careful comparison of his description with that of *Z. carinata* by Herbert and a study of the Hu sketch, living plants and herbarium specimens leave no question that *Z. Tsouii* and *Z. carinata* are identical. As already stated, the latter is widely distributed. Bulbs of *Z. carinata* have been imported from Japan, grown and flowered, and in the Gray Herbarium, Harvard, there is a specimen collected at Yokohama by Maximowicz as long ago as 1862. It is apparent, therefore, that this species has been in the Orient for many years. In the Hu illustration the impression is of a flower with pointed sepals and petals. This is only apparent because their margins are rolled inward as they normally are in flowers just opening. Moreover

4-merous development, five stigmas and other abnormalities are so frequent in *Z. carinata* as to be almost characteristic. Neither capsules nor seeds are illustrated or described and so far as known the species very rarely or never forms seed. Indeed it may be a clon, perhaps a hybrid.

Z. robusta (Herb.) Baker and *Z. Taubertiana* Harms

Zephyranthes robusta (Herb.) Baker dates back more than a century to the time when Herbert (1829) described it as *Habranthus robustus*. Baker (1888) transferred it to *Zephyranthes*. It has been illustrated by Herbert (1829), Loddiges (1831) and Stapf (1927). On the whole these illustrations are good and sufficient for identification of the plant. Its general characters are such as to separate it readily from most other species in the genus. It has large, light pink, declinate flowers and is a valuable ornamental. Harms (1895) described *Zephyranthes Taubertiana* as a new species from a pot-grown plant without stating where it was native, and later published an illustration and a popular description (1896). Careful comparison of available illustrations and descriptions and study of living plants show that *Zephyranthes robusta* and *Zephyranthes Taubertiana* are names applied to the same species and the latter becomes a synonym.

Z. bifolia (Aub.) Roemer and *Z. rosea* Lind.

The status of the West Indian *Zephyranthes bifolia* has been in doubt for many years, the name having been regarded as a synonym of *Z. rosea*. It is so listed in the Index Kewensis (1894) and because of lack of detail in the first and for many years the only description its identity and validity have been questioned. Scant diagnosis of species, lacking in important details, are not unusual among the earlier descriptions of plants belonging to this genus.

The botanical history of *Z. bifolia* begins with a drawing (No. 147) by Plumier of a plant credited to Santo Domingo and Cayenne. This drawing is labeled *Lilio-narcissus bifolius purpureus*. Through the kindness of Professor H. Humbert a photograph of the Plumier illustration, in the Museum National d'Histoire Naturelle, Paris, France, is in hand. It represents a species of *Zephyranthes*. Two views of the same bulb in bloom are shown to bring out the inner and outer characters of the flower. The leaves taper to a sharp point and the longer one exceeds the scape. The peduncle is of medium length. The spathe is longer than the peduncle with the points of its divisions extending above the ovary. The tube is short, and the perianth parts are broadly oval, rounded to their apices. The stigmas extend beyond the anthers.

With a three word description and reference to Plumier's catalogue

and manuscript, Aublet (1775) established the binomial "*Amaryllis bifolius*." From the Plumier sketch, Lamarck (1783) described *Amarillis à deux feuilles* at some length. No allowance was made for variations in the plant not brought out in the drawing; indeed, the description fairly covered only what the drawing showed. Herbert (1837) placed the plant as a variety of *Zephyranthes rosea*, apparently without having seen the Plumier drawing. Roemer (1847) listed *Z. bifolia* as a doubtful species while Kunth (1847) followed Herbert and placed it as a variety of *Z. rosea*. Baker (1888) thought it probably was identical with *Z. rosea*. Apparently all descriptions of this plant and comments thereon were based upon Lamarck's diagnosis of Plumier's drawing until Urban (1907) wrote a new description from specimens collected in Haiti by Picarda (No. 1087) and Buch (No. 366 and No. 599). The description by Urban fits the plant illustrated by Plumier. Specimens collected by von Turckheim (No. 3042) are in the New York Botanical Garden and the Gray (Harvard) Herbaria and by Fuertes (No. 139) in the New York Botanical Garden. Additional specimens are in the National Museum Herbarium, Washington, D. C.

There remains no doubt that *Z. bifolia* is a valid species distinct from *Z. rosea*. It is neither a duplication of *Z. rosea* nor is it a variety of that plant. In *Z. rosea* the leaves are recumbent, bright green, relatively broad and short, rounded at their apices. The peduncle is about twice as long as the spathe. The perianth parts are narrower and more tapered than are those of *Z. bifolia*. The latter is a more robust plant with longer leaves and larger flowers.

In connection with these studies, specimens in the Gray (Harvard) and the New York Botanical Garden Herbaria have been studied. I am indebted to Dr. E. D. Merrill, Director, The New York Botanical Garden, for this opportunity. Specimens in the herbarium of the National Museum also have been examined through the courtesy of Dr. W. R. Maxon. Associate Curator. Dr. L. H. Bailey, Ithaca, New York has furnished references and citations. To all of these my appreciation is due.

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Explanation of Figures

Fig. 1. *Zephyranthes citrina* Baker. Grown from British Guiana bulbs. ×½

Fig. 2. *Zephyranthes carinata* Herb. Native in Mexico; common in southern gardens. ×½

Fig. 3. *Zephyranthes robusta* (Herb.) Baker. Native in Argentina. ×½

Fig. 4. *Lilio-narcissus bifolius purpureus.* Plumier mss. 147. Photo by A. Cintract, of the original in Museum Hist. Nat. Paris.

Fig. 5. *Zephyranthes rosea* Lind. Native in Cuba. Specimens grown in Florida. ×½

FIG. 1

FIG. 2

FIG. 3

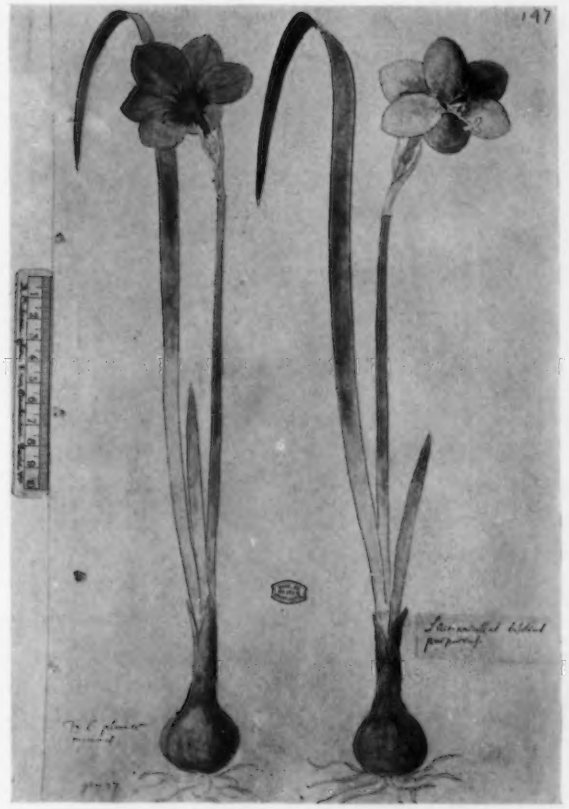

FIG. 4

FIG. 5

The dissociation of Fusarium in soil

C. R. Orton[1]

(with plates 21–24)

The phenomenon in the fungi known variously as "saltation," "variation," "dissociation," "mutation," and "sectoring" has been described by many workers from laboratories throughout the world. The phenomenon is best illustrated by the appearance of sectors of a strikingly different aspect as a colony develops on an agar plate.

Numerous attempts have been made to explain this phenomenon. Some think it may be due to a particular constituent or combination of constituents of the substrate; some have attributed it to hyphal fusions, to "mixochimaera," cytoplasmic inheritance, etc.; by others it has been attributed to high temperatures; and in lieu of any specific evidence many have concluded that "sectoring" is in some way bound up with the artificial culture of these organisms.

While such "dissociants" are well known to vary widely from their parental stocks in both physiologic and pathogenic behavior, few investigations have been made to determine what part these "dissociants" play in the development of new parasitic and saprophytic forms under conditions as they exist in nature. In fact heretofore it has been uncertain whether this phenomenon existed outside the cultural conditions of the laboratory.

The first question to be settled, if possible, is whether dissociation takes place in the soil. The investigations of Sleeth (1934) indicated that it does. He reports two instances of dissociants recovered from plants growing in infested flats, which were identical with dissociants which had appeared previously in laboratory plates from the same strain which was used for inoculating soil in the flats. While this was strong evidence of dissociation in the soil, it was not considered adequate proof for the reason that the flats were open to contamination. It seemed necessary to conduct an experiment which would obviate the possibility of contamination factors and at the same time answer this question. Furthermore it opened the question whether those dissociants actually originated in the soil or whether they may have originated in the seedlings.

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I wish to acknowledge my indebtedness to Dr. Bailey Sleeth, Mr. Paul Smith, Miss Genevieve Clulo and Mr. Oliver Orton who have assisted in the culture work. Especially am I indebted to the National Research Council, Division of Biology and Agriculture for the Grant-in-Aid which made it possible to carry out these studies.

METHODS

The set-up of the experiment which began in March, 1933, was as follows: Four pounds of prepared greenhouse soil containing approximately 25 per cent moisture was added to each of 32 Erlenmeyer flasks of 2000 cc. capacity and sterilized in autoclave for one hour periods at 15 pounds pressure on three successive days.

For this experiment four strains of *Fusarium niveum*, two strains of *F. vasinfectum*, and one of *F. tracheiphilum* were selected. These seven strains were grown on rice in petri dishes until the entire mass of rice was well permeated by the fungus. Two petri dish cultures of the same strain were used to inoculate four flasks—one-fourth of each dish to one flask, each flask requiring an amount equal to one-half of the culture in a plate. The culture in each case was well mixed with the soil.

The flasks were closed with rubber stoppers containing two holes plugged with sterilized cotton to allow gas exchange but preventing contamination. Paraffined paper cups were inverted over the flask necks to aid in keeping out dust and other sources of contamination.

Two flasks of each of the seven strains plus uninoculated checks were placed in the greenhouse (unshaded) and a like number in a cold frame outside (shaded).

In August, 1933, sixteen additional flasks were prepared as follows and placed in the greenhouse laboratory in shade:

Flask No.	*Size*	*Amt. Soil*	*Treatment*	*pH after Sterilization*
1a	2000 cc.	1000 gm.	$CaCO_3$, 3 gm.	6.58
1b	"	"	" "	6.77
2a	"	"	" 6 "	7.04
2b	"	"	" "	7.00
3a	"	"	H_2SO_4, 1 cc.	5.00
3b	"	"	" "	5.50
4a	1000 cc.	600 gm.	$Ca(NO_3)_2$, 3 gm.	6.05
4b	"	"	" "	6.06
5a	"	"	KNO_3, 3 "	6.10
5b	"	"	" "	6.06
6a	"	"	Oatmeal, 20 gm.	6.42
6b	"	"	" "	6.45
7a	"	"	Untreated, sterilized	6.40
7b	"	"	" "	6.42
8a	"	"	" not sterilized (uninoculated)	7.17
8b	"	"	" " " "	7.07

The pH was determined by Dr. G. G. Pohlman, using the quinhydrone electrode method.

The *a* series with exception of 8a, was inoculated with *Fusarium niveum*, strain 20, and the *b* series with exception of 8b with *Fusarium vasin-*

fectum, strain 104, by transferring the mycelium and spores of each strain from one 2-weeks old petri plate culture to 200 cc. of sterile water. This inoculum was thoroughly shaken and 10 cc. of the spore and mycelial suspension added to each flask. In this experiment the soil in the flasks was near saturation. The flasks were stoppered and protected like those in the March experiment.

At approximately monthly intervals a sample of the soil was taken from each flask in both experiments and plated on Leonian's modified agar of the following composition:

1 gram potassium acid phosphate
1 gram magnesium sulphate
3 gram proteose peptone
15 gram dextrose
20 gram Bacto-agar in 1000 cc. distilled water

Careful attention was directed to a study of the resulting colonies from which three groupings were made: (1) colonies like the parental strain; (2) colonies unlike the parental strain "colony dissociants"; and (3) colonies of the parental strain showing sectorial dissociation.

DISCUSSION

Particular emphasis is placed upon the second group, which records the number of entire colonies different from the parent. When an entire colony, differing in marked characteristics from the parental type, appeared among the normal colonies on the same plate there appears to be no reasonable doubt that it originated in the soil and could be attributed in no manner to the influence of the culture medium or other ecological factors influencing the plate culture.

The sectorial dissociants recorded under group 3 are not so clearly delimited as to their origin. The visual evidence places their origin in the petri dish, but the fact that they occurred repeatedly from the same flask is some evidence that they originated in the flask. However, this question may be considered unsettled for the present.

In a number of cases these "colony dissociants" were like the sectorial dissociants which appeared both from the soil as recorded in group 3, as well as from stock cultures in the laboratory. (See 11a, 20a, 20b, 104a, 104c).

The data are considered conclusive in showing that several strains of *Fusarium niveum* may dissociate as readily in soil as upon laboratory media. We believe this has a direct relationship to the large number of strains which are distributed in nature throughout our watermelon soils.

TABLE 1

Soil flasks in greenhouse (G) exposed to sun and outside in shaded cold frame (C.F.) for 22 months

STRAIN	ENVIRONMENT	TOTAL COLONIES	(1) LIKE PARENT	(2) UNLIKE PARENT "COLONY DISSOCIANTS"	(3) COLONIES SHOWING SECTORING	DESIGNATION AND DISTRIBUTION OF DISSOCIANTS
5	Greenhouse	450	447	3	0	5a, 5b, 5aa;
5	Cold Frame	450	448	2	0	5b, 5aa;
11	G.	450	427	(a) 3(21)	(a)2(2)	(b)11a(5) 11b(5) 11A1(11): 11a(1) 11c(1)
11	C.F.	450	449	1	0	11b
16	G.	450	448	1(2)	0	16a(2)
16	C.F.	450	449	0	1	16a
20	G.	450	438	3	3(9)	20a(1) 20b(1) 20c(1); 20b(4) 20b(3) 20d1(2)
20	C.F.	450	444	3	3	20T1(1) 20T2(1) 20T3(1); 20a(1) 20d(1) 20a(1) 0
101	G.	450	450	0	0	*F. vasinfectum* from Dr.
101	C.F.	450	450	0	0	V. H. Young
103	G.	450	450	0	0	*F. vasinfectum* from Dr.
103	C.F.	450	450	0	0	C. D. Sherbakoff
105	G.	450	447	0	2(3)	105a(1) 105b(2)
105	C.F.	450	450	0	0	*F. tracheiphilum* from C.D.S.
Checks	G.	0	0	0	0	
Checks	C.F.	0	0	0	0	
Totals	G.	3150	3107	10(29)	7(14)	
	C.F.	3150	3140	6	4	

(a) Figures outside parenthesis record number of distinct dissociants in this class secured throughout the duration of the experiment. Figure inside parenthesis record the number of times such dissociants occurred.

(b) The figures in parenthesis in last column record the number of times each dissociant appeared during the period covered by the experiment. The semicolon separates colony dissociants from sectorial dissociants.

Also it is probable that dissociation is responsible for the variation in pathogenicity of the strains occurring naturally. Otherwise how can we account for the variability in pathogenicity of the dissociants secured by Sleeth? Some of these apparently are identical with sector dissociants produced in stock cultures in the laboratory and which have been tested also for pathogenicity.

There is evidence that some strains are much more stable than others with respect to their tendency to produce dissociants. Two strains, 101 and 103, both of which were from wilted cotton plants and were identified when sent to me as *F. vasinfectum*, produced no dissociants during a period of 22 months. On the other hand strain 104, also *F. vasinfectum* from cot-

TABLE 2

Culture flasks stored in shade in greenhouse laboratory for 17 months

STRAIN	SUPPLEMENTAL TREATMENTS	TOTAL COLONIES	(1) LIKE PARENT	(2) UNLIKE PARENT "COLONY DISSOCIANTS"	(3) COLONIES SHOWING SECTORING	DESIGNATION AND DISTRIBUTION OF DISSOCIANTS
20	Same as 104	960	960	0	0	
104	$CaCO_3$, 3 gm.	120	115	(a)2(5)	0	(b)104a(4) 104c(1)
104	$CaCO_3$, 6 gm.	120	120	0	0	
104	H_2SO_4, 1 gm.	120	118	1(1)	(a)1(1)	104a 104a
104	$Ca(NO_3)_2$, 3 gm.	120	120	0	0	
104	KNO_3, 3 gm.	120	120	0	0	
104	Oatmeal, 20 gm.	120	90	2(20)	4(10)	104a(3) 104c(17); 104a (1) 104b(2); 104b1(1) 104c(6)
104 (ck)	Untreated, Sterilized (inoculated)	120	120	0	0	
Check	Untreated, sterilized (uninoculated)	0	0	0	0	
Totals		1920	1873	5(26)	5(11)	

(a) and (b). See footnote table 1.
Strain 20 = *Fusarium niveum*
Strain 104 = *Fusarium vasinfectum*

ton, has produced two distinct dissociants, 104a and 104c, which have appeared 26 different times in three separate flasks. It appears that stability and instability are characteristic of particular strains and are purely relative judging from the results of studies extending over several years in our laboratory. Some isolants have continued to be stable as long as four years and have then dissociated.

The results show more dissociation in the soil in flasks stored in the greenhouse, where they were exposed for 22 months to intense sunshine and high temperatures, than in the soil in flasks stored in a cold-frame, where they were shaded and subjected only to cool and less fluctuating temperatures. There may be some doubt as to the significance of these differences but they are suggestive of results in Barnes' (1930) laboratory where high temperatures have been reported as inducing "variations."

The results obtained with strain 104 in soil which received supplemental treatments indicate that certain of these treatments may have had some influence upon the production of dissociants. The most outstanding result came from the oatmeal-treated flask, where four distinct dissociants were produced. The check flask produced no dissociants. Possibly the presence of abundant organic matter in the soil may exert some influence.

The substrate in this flask showed pH 6.45. I see no particular significance in the results produced in the flask containing 1 gram H_2SO_4 with pH 5.50. The failure of strain 20 to produce dissociants in the supplemental treatments is not explained. Possibly a continuation of this test over a longer period would have given results. This test was continued only for 17 months in contrast to the 22 months' duration of the other experiment.

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Explanation of plates 21–24

Surface characters were taken from upper surface of 7-day-old colony.

Color characters were taken from the lower surface of colony at same age.

Color references are to Maerz and Paul, Dictionary of Color, McGraw-Hill Book Company, 1930.

Plate 21

5—Surface: smooth; color: plate 44; G1, margin lighter

5a—Surface: thin growth of aerial mycelium; color: plate 10; J2

16—Surface: smooth; color: plate 9; A2

16a—Surface: aerial mycelium cottony, but not thick; color: plate 42; I1

105—Surface: much lilac tinted aerial mycelium, fluffy; color: plate 47; J6

105a—Surface: smooth, tendency towards aerial mycelium; color: center, Plate 47; J9, margin, plate 46; between K2 and L2

Plate 22

104b—Surface: scant, cottony, aerial mycelium; color: plate 47; H2, lighter margin

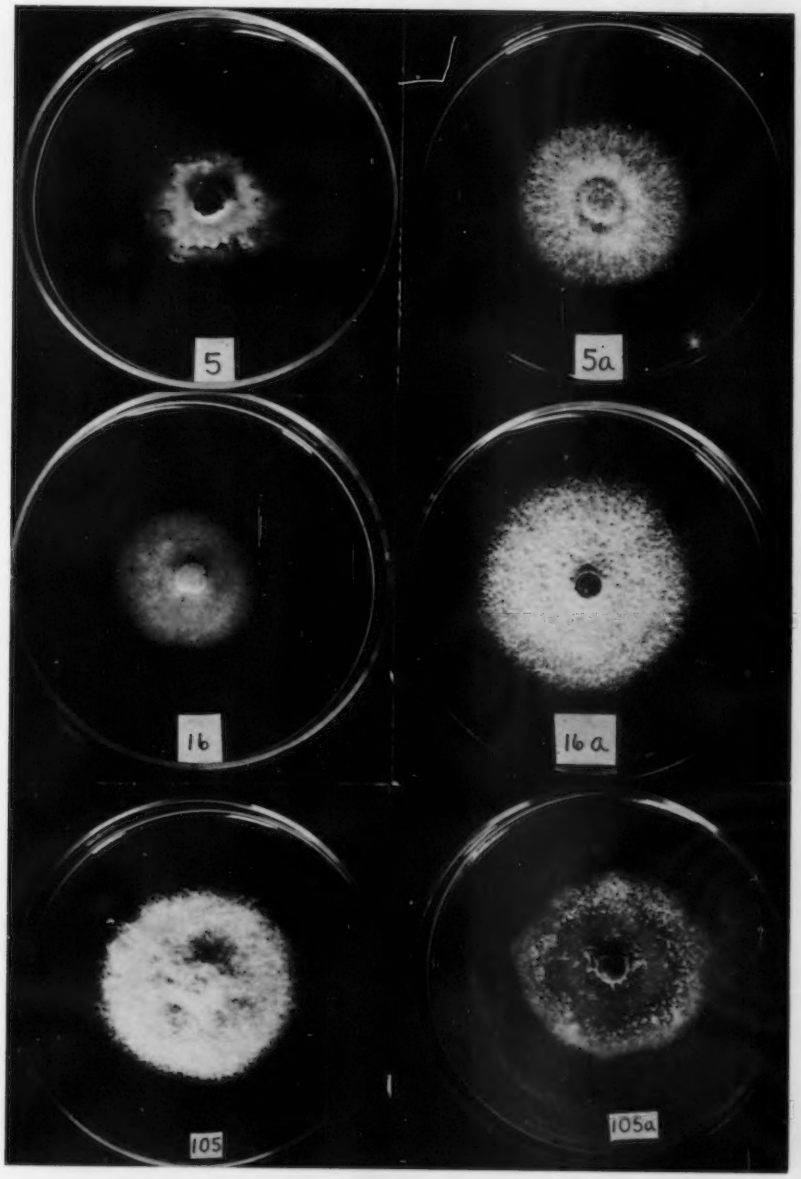
104b1—Surface: good growth of cottony, aerial mycelium; color: plate 48; L12

104c—Surface: much cottony, aerial mycelium, colored; color: plate 47; L8

11—Surface: smooth, slight tendency toward aerial mycelium; color: plate 46; between K2 and L2

11a—Surface: smooth, slight tendency toward aerial mycelium; color: plate 47; H5

11b—Surface: small amount of cottony aerial mycelium; color: plate 48; L3



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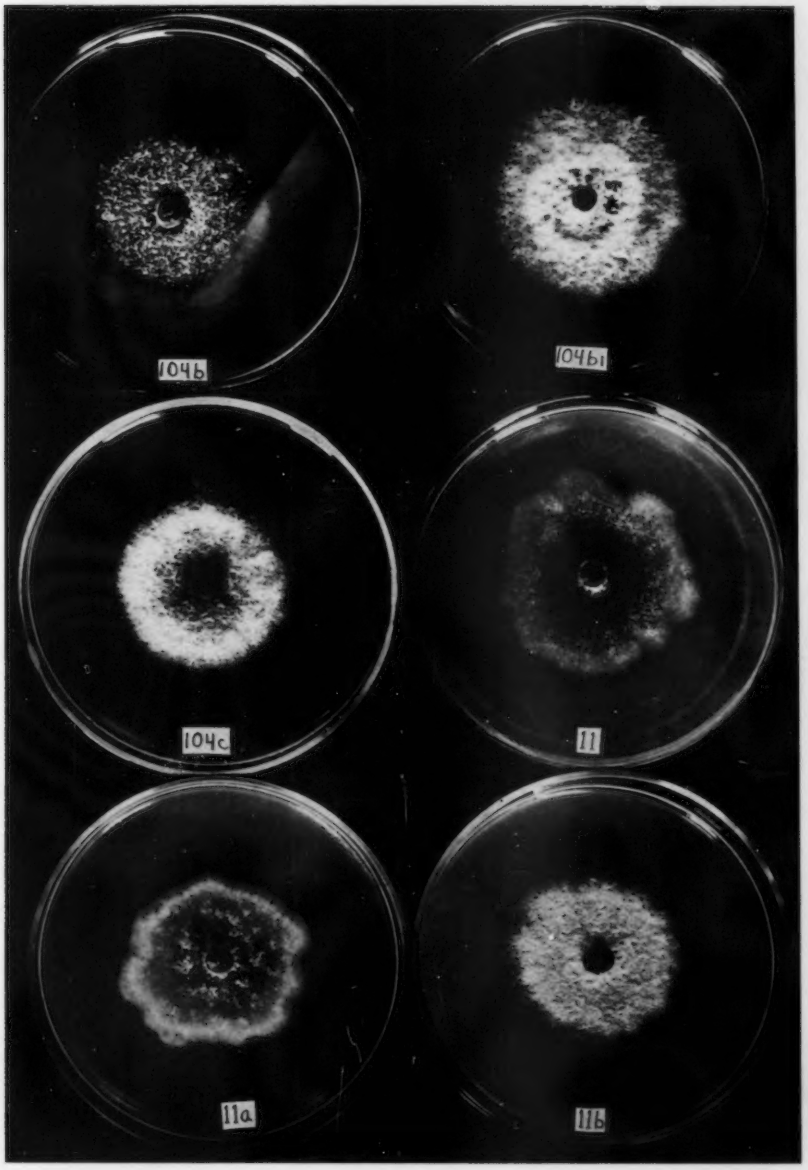

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Plate 23

20—Surface: scant aerial mycelium; color: plate 48; L1, lighter margins, striations present

20a—Surface: good, cottony growth of aerial mycelium; color: plate 48; H12, margins lighter

20b—Surface: luxuriant, fluffy, aerial mycelium, tinted pink near the center; color: plate 47; J3 at center, plate 5; E3 at margins, striations present

20c—Surface: aerial mycelium scant, matted; color: plate 48; L1, faint striations present

20d—Surface: smooth; color: plate 43; F1

20d1—Surface: cottony aerial mycelium, colored near center; color: plate 47; L5

Plate 24

20T1—Surface: scant, cottony, aerial mycelium; color: plate 48; L1, lighter margins, striations present

20T2—Surface: smooth; color: plate 43; E1

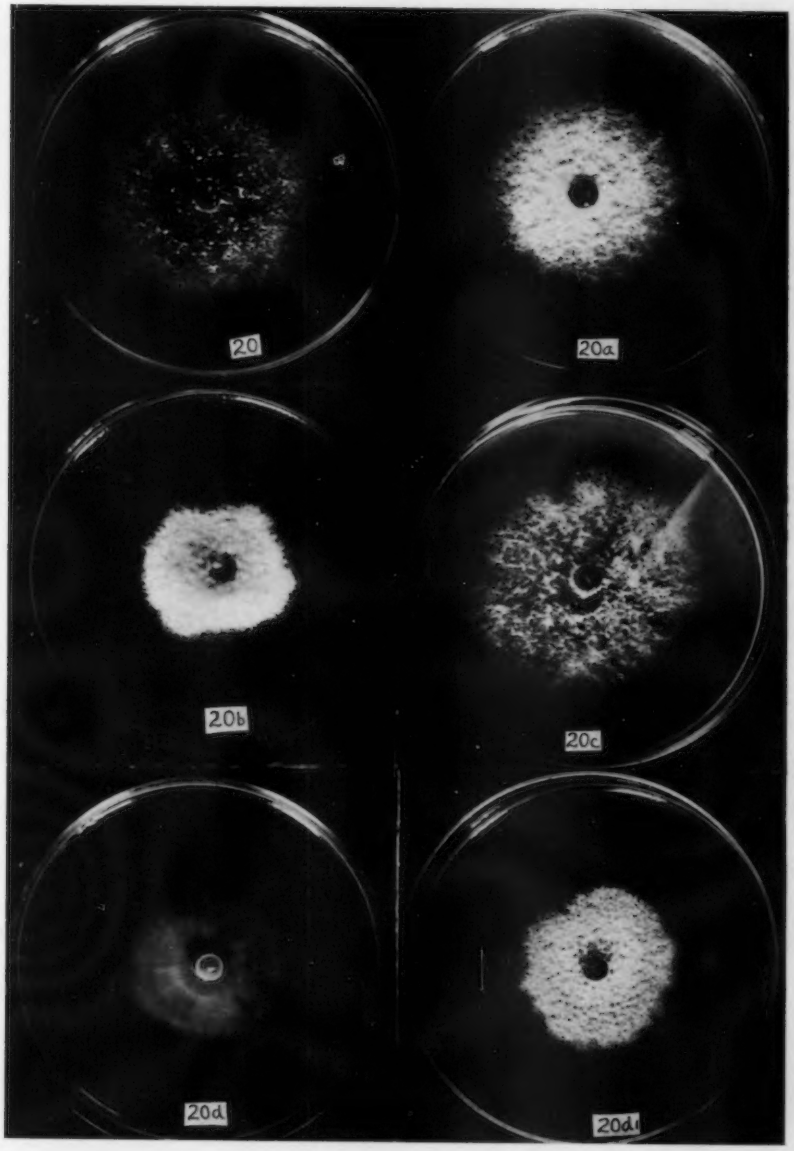
20T3—Surface: nearly smooth, with a slight tendency towards aerial mycelium; color: plate 46; I1

20a—Surface: thick, close growth of aerial mycelium; color: white

$\overline{0}$

104—Surface: fine growth of cottony mycelium; color: plate 43; E1

104a—Surface: cottonv aerial mycelium; color: plate 47; J6



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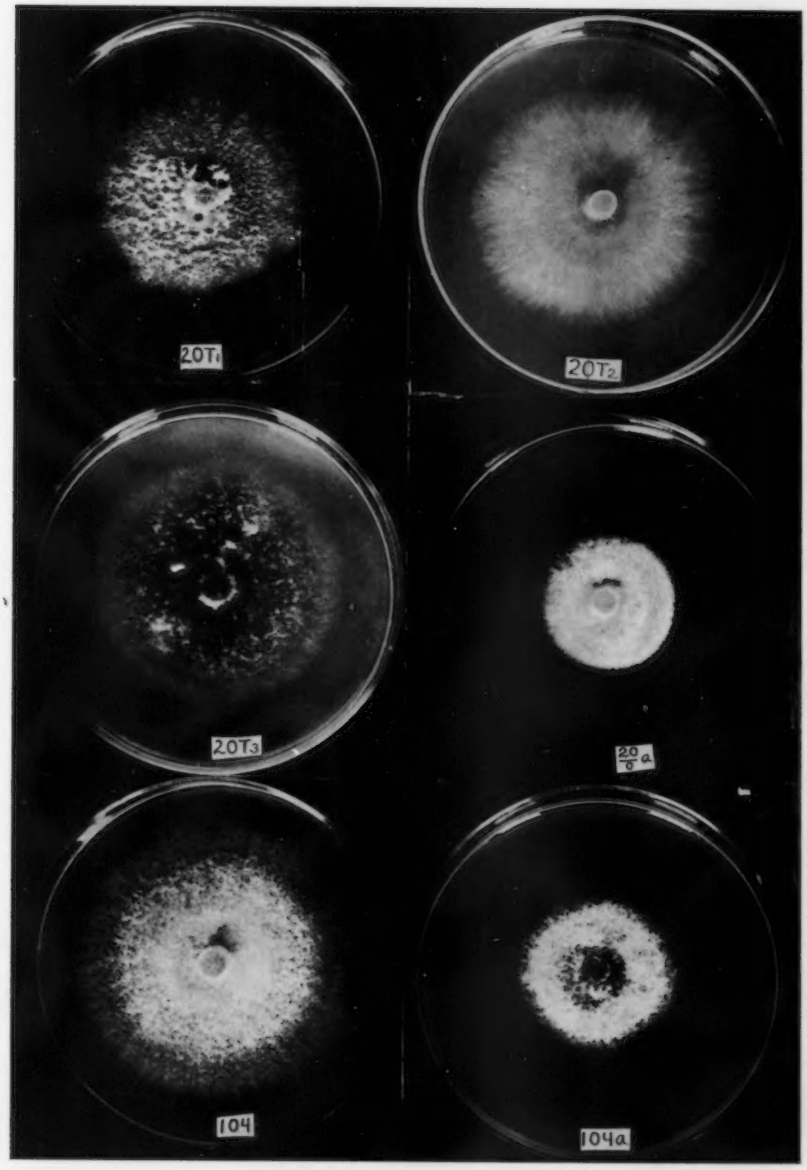

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INDEX TO AMERICAN BOTANICAL LITERATURE

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